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THE FUNCTIONS OF THE SPIRACLE OF THE SKATE

HERBERT W. RAND

In the latter part of September, 1904, I spent a few days at the Woods Hole laboratory of the United States Bureau of Fisheries for the purpose of making a study of certain blood vessels of the skate. At that late season the Fisheries laboratory had abandoned its fish traps and I was supplied with material through kindness of officials of the Marine Biological Laboratory, which was still maintaining a trap in Vineyard Sound. One afternoon this trap was hauled and some seven or eight common skates (*Raja erinacea*) were taken. The skates were thrown with numerous other fish into the bottom of a skiff which was towed back to the laboratory by the steam launch,— a distance of about a mile. Arrived at the laboratory, I picked out the skates and threw them into a large shallow tank for the purpose of washing from them the sand and debris which had become attached to them in transit. In view of the fact that the fish had been out of the water nearly an hour and had been subjected to no very careful treatment, it did not occur to me but that they were dead, or at least beyond the possibility of reviving. By means of a hose I turned upon them a copious stream of cold sea water and then I noticed, for the first time, that feeble respiratory motions were in progress. As I continued to play the water over the fish the respiratory motions became stronger. Shortly one skate slid over the opening of the

outlet of the tank, closing it, and in a few moments a half inch of water had accumulated over the bottom of the tank. Thereupon the skates set up an energetic spouting of water from the spiracles, — a mode of behavior which had never before come to my notice. At frequent intervals a large stream of water was ejected from each spiracle, rising vertically to a height of one or two inches. (The fish were of uniform size,— about a foot in width across the pectoral fins.) The animals were not submerged, it should be remembered, but were less than half covered with water, most of the dorsal surface, including the spiracular region, being well out. The vigor and frequency of the spouting and the fact that so many skates were doing it at the same time produced an effect striking enough to compel attention. No doubt this behavior has been observed previously by others. A "Spritzloch" is certainly a spout-hole. But I could recall having met only the briefest reference to the use of the elasmobranch spiracle in respiration, so I postponed the fate of some of the skates and placed them in an aquarium supplied with running sea water, with a view to watching their respiratory movements. During the next few days I observed the fish as I could, but other work had precedence, so that I was unable to carry on any systematic study of their behavior. However, my impromptu experiments brought to light one or two facts which seem to me worthy of mention.

As must be well known, the modified first visceral cleft (spiracle) serves in the skate chiefly as an incurrent opening for the respiratory stream. So far as this function is concerned, as pointed out by Garman ('74), the spiracle is probably of greater importance in the rays than in the sharks, owing to the fact that the rays, for the most part, lie flat upon the bottom of the sea, and this habit places the mouth at a disadvantage as an incurrent respiratory opening, while in the perpetually roving sharks such is not the case. These facts are very likely connected with the fact that the spiracles occur as large openings in all the rays while in many of the sharks they are either very small or completely closed.

Many writers make the statement that water may pass either into or out from the mouth by way of the spiracle. Garman ('74) notes that, whereas the sting-rays have in the spiracular passage a valvular fold preventing outflow, in the common skate no such

structure is present, so that water may pass either way. Duméril ('65–70, tome 1, p. 210) states that water usually enters the mouth through the spiracle, but less frequently passes in the reverse direction.

While at rest on the bottom of an aquarium, the skate slightly elevates the head above the surface of the bottom in the manner described in Brehm's Thierleben (Brehm, '79, p. 387), which may well be quoted : "Abweichend von anderen Bodenfischen liegen sie mit dem Vordertheile ihres Leibes niemals fest auf, sondern stützen sich so auf ihre Brustflossen, dass in der Mitte ein Hohlraum bleibt." Continuing, Brehm's account says, "Um die Kiemen mit Wasser zu versorgen, öffnen sie ihre Athemlöcher, indem sie den Kolben zurückziehen, füllen die Kiemensäcke, schliessen die Athemlöcher und treiben das verbrauchte Wasser durch die Kiemenspalten nach aussen." According to my observations the skate takes in water not only by the spiracle but also through the mouth, although considerably more water enters through the spiracle than through the mouth.

When fully open the external aperture of the spiracle in the common skate is nearly elliptical in outline, but the curvature of its anterior margin is much greater than that of its posterior margin. The anterior lip of the opening bears the rudimentary gill and the closing of the spiracle is effected mainly by the contraction of this gilled lip, while the posterior lip, being nearly straight when relaxed, contracts but little.

In ordinary respiration the spiracle opens and closes with pendulum-like regularity. During one of the prolonged resting periods of the fish, the interval between successive openings is longer than when the fish is active, and the spiracle is not opened wide,— indeed, the opening may be only a narrow slit. During more active respiration the anterior lip of the spiracle moves back and forth with a quick decisive motion and the spiracle is opened to its utmost width. As the spiracular valve opens, the branchial region is expanded and a strong current of water is drawn in through the spiracle, the external branchial apertures meanwhile being tightly closed. At the same time that the spiracle is open, the mouth also is opened more or less and a certain quantity of water enters. I satisfied myself as to the inward current at the mouth

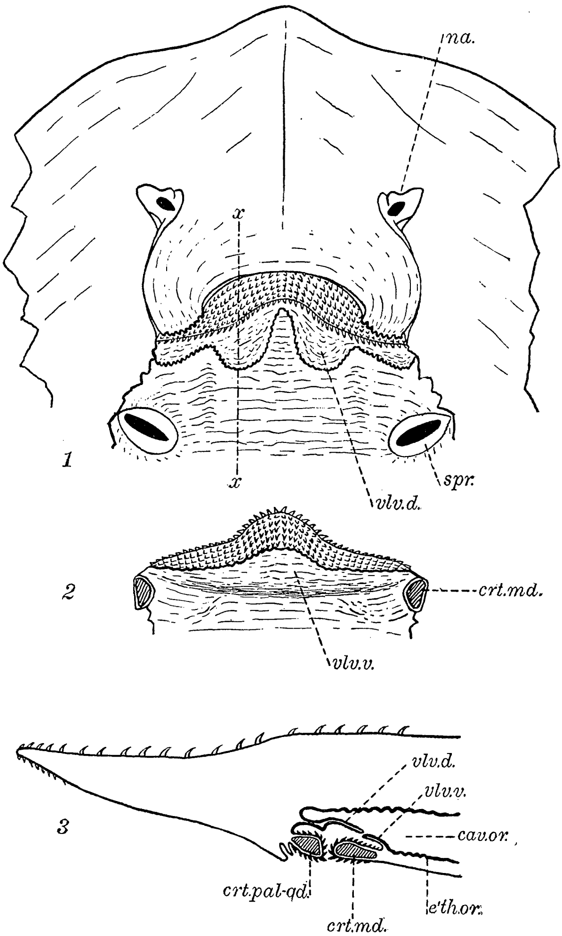
by watching the movement of solid particles suspended in the water in the vicinity of the mouth. Much the greater volume of water, however, appears to enter through the spiracle.[1] During an expiration the spiracle is shut, while the mouth tends to close but does not close tightly. The mouth action was always a little sluggish as compared with the action of the spiracle, especially in opening. As nearly as I could determine, mouth and spiracle closed together, but the opening of the mouth was slightly later than that of the spiracle. As spiracle and mouth close, the branchial region is contracted and the water contained in the gill chambers is forced out through the gill clefts.

That water does not flow out through the mouth as well as through the gill clefts during an expiration is probably due to the action of a well developed respiratory valve similar to those described for teleosts by Dahlgren ('99). The dorsal flap of the valve (Figures 1 and 3, *vlv. d.*) is a conspicuous bilobed fold of the oral membrane, while the ventral or mandibular flap — a less extensive fold — is broadest in the median region of the lower jaw and becomes much narrower towards the sides of the mouth. Judging from the relative widths and the positions of the two parts of the valve, it appears that the prevention of outflow through the mouth must depend mainly upon the action of the dorsal flap. Garman ('74) mentions only the dorsal one of these two folds.

The elevation of the forward end of the fish above the surface on which it rests would seem to facilitate the respiratory process.

[1] To observe these respiratory movements I put a fish in a large rectangular flat-bottomed glass vessel. The vessel was placed upon a high table so that one end projected some distance beyond the edge of the table. The fish was induced to lie with its head in the overhanging part of the vessel. I found that an object held just underneath the mouth could be seen directly through the head of the fish by looking, at the proper angle, into the spiracle as it opened, and, similarly, an object held just above the spiracle could be seen by looking upward into the mouth as it opened. This was sufficient proof that mouth and spiracle were open at the same time. In order to see the dorsal and ventral surfaces of the head at the same time so that the action of spiracle, mouth and gill clefts could be observed simultaneously, I viewed the spiracle by total reflection from the surface of the water. Having the water at a certain depth and looking upward from underneath the overhanging vessel at just the proper angle, I could see by reflection the dorsal surface of the head with sufficient clearness, while at the same time I had a direct view of the ventral surface of the head.

Is the spiracular current ever reversed — that is, does the spouting occur — in normal respiration? To answer this question



RESPIRATORY VALVE OF *Raja erinacea.*

FIG. 1.— Ventral aspect of the head of a skate, the lower jaw and floor of mouth having been removed so as to show the roof of the mouth and the dorsal flap of the respiratory valve (*vlv. d.*). *na.*, nostril; *spr.*, oral aperture of spiracle.

FIG. 2.— Lower jaw and anterior part of floor of mouth, showing the ventral or mandibular flap of the respiratory valve (*vlv. v.*). *crt. md.*, cut end of mandibular cartilage.

FIG. 3.— Parasagittal section of the jaws at the position of the line *x x*, Figure 1. *cav. or.*, mouth cavity; *crt. md.*, mandibular cartilage; *crt. pal-qd.*, palato-quadrate cartilage; *e'th. or.*, oral epithelium; *vlv. d.*, dorsal flap, and *vlv. v.*, ventral flap, of respiratory valve.

I watched the respiration of skates in aquaria supplied with running water, observing the fish at times when they had not been disturbed in any way for several hours. At such times the rate of respiration was always slow,— usually from 22 to 30 inspirations per minute. At fairly regular but long intervals there occurred a break in the regular alternation of inspiration and expiration. This break was brought about in the following way. Immediately after an inspiration (and therefore in a period ordinarily marked by a contraction of the pharynx with closed spiracle and open gill clefts) the spiracle remained open and the gill clefts remained tightly closed while a particularly vigorous contraction of the pharynx caused the contained water to be ejected forcibly from the spiracle. It is apparently by muscular action that the gills are kept closed during the spouting, since the pressure of the water in the gill chambers would tend to force open the external valves. During the spouting the mouth was open, as it is during inspiration, and some water escaped from it, but very little as compared with the amount ejected from the spiracle. It is doubtless due to the respiratory valve that the outflow from the mouth is not greater. The contraction which caused the spouting was immediately followed by an expansion of the pharynx, the spiracle still remaining open and the gill clefts closed, and respiration then proceeded in the usual way. In animals which had been at rest for several hours, the rate of respiration being then at its lowest, the spouting occurred at intervals of five to ten minutes.

Having found that spouting is a feature of normal respiration in a resting fish, I next sought to discover what part the spouting plays in the respiratory process. With this end in view, I observed the fish under other conditions than rest.

Effects of Exercise.— The rate of respiration in a fish varies with the degree of activity. To induce rapid respiration I caused the fish to take exercise. This was effectively done by grasping and holding the skate firmly by the tail. The most violent efforts are made to swim away from the detaining grasp. Following are accounts of several experiments in which the rate of respiration was caused to vary.

(1) A skate had been undisturbed over night in an aquarium supplied with running sea water. When first observed in the

morning the fish was at rest, the respiration being very slow and the spouting infrequent, as described above for the resting condition. I have no record of the precise rates in this case. The fish was then exercised and immediately removed to a shallow tray of water for easier observation. The rate of respiration was markedly increased, rising to 47 inspirations per minute, and a spouting occurred on the average after every nineteenth inspiration, that is, a little oftener than twice a minute. This average was obtained by counting the number of inspirations within a period covered by eleven successive spouts. The actual number of inspirations between two successive spouts varied from 15 to 23.

In a similar case the rate of respiration while at rest was 22 inspirations per minute, with spouting at intervals of several minutes. After exercise the rate of respiration was 39.5 per minute, with a spouting after every seventeenth inspiration, or at the rate of 2.3 spouts per minute.

(2) A skate which had been undisturbed, so far as I know, for two days was found resting quietly against the side of the aquarium. The rate of respiration and the frequency of spouting were determined. Then the fish was exercised vigorously for five minutes, after which it was given five minutes to become quiet so that observations could be made. Following are the results of the experiment.

	No. of Inspirations per Minute	No. of Inspirations between Spouts	No. of Spoutings per Minute[1]
Resting	30	246	0.12
After exercise	47.5	67	0.71
Increase	58%		500%

(3) A skate which had been under experiment was allowed to rest for about an hour. At the end of that time the rates of respiration and spouting were determined. Then during the next half hour the fish was subjected to some annoyance by irritation

[1] The rate of spouting is thus expressed for the sake of ready comparison with the rate of respiration (first column). Thus, a spouting rate of 0.12 means that the spouting occurred at intervals of about eight minutes.

of the spiracle and neighboring parts (see page 299). After these experiments the fish was exercised vigorously for a minute or so, after which the rates were again observed. Following are the results of the experiment.

	No. of Inspirations per Minute	No. of Inspirations between Spouts	No. of Spoutings per Minute
Immediately after one hour's rest	47	55	0.85
After a half hour's annoyance, followed by brief violent exercise,	63	42	1.5
Increase	34%		77%

The high respiratory rate (47) immediately after the hour's rest apparently means that the fish had not recovered from the effects of the experiments which preceded that hour, a rate as high as 57 having been induced in the course of these experiments.

(4) In a skate immediately after exercise, conditions were as shown in the following table.

	No of Inspirations per Minute	No. of Inspirations between Spouts	No. of Spoutings per Minute
(a)	49.5	49	1.0

This skate was then left undisturbed about three hours in a small vessel of water, which was not changed during that time. At the end of the three hours the rates were as follows.

	No. of Inspirations per Minute	No. of Inspirations between Spouts	No. of Spoutings per Minute
(b)	39	78	0.5
Decrease in rates, comparing (b) with (a)	21%		50%

Immediately after the record (b) was obtained, the fish was exercised and put into well aerated water. After five minutes (to allow the fish to become quiet enough for observation) the conditions were: —

	No. of Inspirations per Minute	No. of Inspirations between Spouts	No. of Spoutings per Minute
(c)	49	22.5	2.2
Increase in rates, comparing (c) with (b)	26%		340%

In this experiment the rates of respiration and spouting are influenced by two factors, exercise and the quality of the water, and the effects of these two factors can not be separated in the results. The experiment is cited because it shows strikingly, and in accord with other experiments, that, as the rate of respiration rises and falls, the rate of spouting likewise rises and falls, but in much greater proportion.

(5) Another observation shows the effect of quiescence. A skate immediately after exercise breathed 40 times per minute and spouted twice per minute. After three hours' quiescence (during the first hour of which the fish was extremely restless), the frequency of breathing had *decreased* 44%, while the frequency of spouting had decreased 68%.

In several other experiments similar to those just described the same general results were obtained. Fish which had been resting quietly for several hours were found to breathe from 22 to 30 times per minute, while the spouting occurred at intervals of several minutes. After vigorous exercise the frequency of breathing was always increased to a rate between 40 and 60 per minute and the spouting occurred once per minute or oftener. Thus, when the rate of respiration becomes more rapid as the result of exercise following a period of rest, the frequency of spouting is increased also, *but in much greater proportion.* A very rough average, from all of the observations taken together, shows that, whereas the rate of respiration is increased about 100%, the rate of spouting is increased at least 500%.

With quiescence, the rates of respiration and spouting drop towards the low resting rates, but the spouting rate falls off relatively much more rapidly than the rate of breathing.

Effects of Partial Asphyxiation.— Is the frequency of spouting affected by partial asphyxiation? The behavior of the fish when first brought into the laboratory suggests this question. The following experiments were made.

(1) A skate was put into a rectangular glass vessel measuring about 12 by 18 inches, containing sea water to the depth of about 3 inches. The fish was allowed to become quiet and then was left undisturbed for two hours, during which time a copious stream of water was flowing into the vessel. At the end of this period the animal was found resting quietly, respiration being at the rate of 22 per minute, while spouting occurred at very irregular intervals averaging about $1\frac{1}{3}$ minutes.

The stream of running water was now shut off and the fish was left in the vessel without change of water for about three hours. During the earlier part of this time there were alternate periods of quiet and unrest. In one of the periods of quiet, the respiration was slow and the spiracle was only slightly opened. But after a minute or two of these resting conditions, respiration became markedly quickened, the spiracle being opened wide at each inspiration, and shortly the fish raised its head and began to swim about, usually trying to swim up the low vertical side of the aquarium so that the head was thrust out of the water. This activity lasted usually less than a minute, after which the fish dropped to the bottom of the aquarium and became quiet, the respiration at once slowing down to the normal resting rate. Sometimes the performance was varied in that the quickened respiration which marked the close of an interval of rest was followed, not by the swimming activity, but by a vigorous spouting, after which slow respiration was resumed. At still other times the period of unrest was marked by both the swimming and the spouting. Occasionally the spouting occurred also in the resting intervals.

During the second hour after the incurrent stream of water was shut off the alternate periods of rest and unrest continued. The rate of respiration, however, gradually increased, reaching a maximum at the end of the second hour when the fish was breathing 59 times per minute and spouting about once per minute. Respiration was equally rapid during rest and unrest. The activity was often much more violent than in the first hour of the experiment.

In the third hour of the experiment the rate of respiration diminished with increasing rapidity. Following is the record (the running water having been shut off at 1.00 P. M.).

3.00 P. M.	Rate	of	respiration	59	per	minute
3.20 "	"	"	"	57	"	"
3.45 "	"	"	"	50	"	"
4.00 "	"	"	"	40	"	"

The spouting continued at the rate of about once per minute. The resting periods were considerably longer than in the preceding hours and the activity was less violent. The fish evidently was becoming sluggish. Returning at 4.10 to observe the fish, I found the respiration obviously much slower and rapidly diminishing in frequency. Before I could determine the rate the respiratory motions suddenly became very irregular and spasmodic and then the action of the spiracle abruptly stopped. I waited, perhaps half a minute, and then, fearing a premature end to the experiment, I turned into the aquarium a stream of water, washing it about the head of the fish. Within a minute feeble and slow respiratory movements began, *shortly followed by four vigorous spoutings in rapid succession.* Respiration quickly became stronger and its rate increased rapidly, reaching 48 per minute at 4.22 o'clock. The rate of spouting, at the same time, was 1.5 per minute, an increase of about 50% over the rate at 4.00 o'clock.

At 4.29 the fish was taken out of the water and left lying on the table top. For several minutes it struggled vigorously, but at the end of eight minutes the respiratory motions had ceased and there was little muscular reaction anywhere—the fish was quite limp. The heart, however, was beating strongly. Then the animal was put into well aerated sea water. At first no sign of returning activity appeared. The spiracle was wide open and motionless. I therefore began kneading the gills and directed a stream of water into the spiracle. Almost immediately very weak, slow and irregular spiracular motions began, and in the course of two minutes regular respiratory movements were in progress, although still weak and very slow. The spiracle did not close tightly, so that some water escaped from it at each expiration. This was not regarded as spouting. The action of the spiracle rapidly quickened and strengthened, and about four minutes after the fish was returned to water I began to count the rate of spouting which was then occurring frequently. The count was made through three successive minutes. During the first minute

the spouting occurred five times, while for the entire period of three minutes there were, on the average, four spoutings per minute. At the end of the three minutes the rate of respiration was found to be 41 per minute.

(2) Following is the record of another experiment.

10.00 A. M. A skate was removed from the water.

11.15 A. M. Feeble respiratory motions of gill chambers and spiracles still in progress at the rate of 28 per minute. The spiracle is continuously wide open, its anterior lip contracting very slightly at each expiratory movement. The mouth is continuously shut.

11.20 A. M. The skate is put into well aerated sea water.

11.21 A. M. The spiracular action is stronger and weak mouth action begins.

11.25 A. M. The spiracle closes completely at each expiratory movement.

	Inspirations per Minute	Inspirations between Spouts	Rate of Spouting
11.30 A. M.	35	25	1.4
11.39	41	39	1.0
11.47	47.5		
11.48 (The first swimming motions occurred.)			
12.12 P. M.	57	76	0.75
2.00	47	55	0.85

These experiments, then, so far as they go, indicate that, under conditions of gradual approach toward asphyxia (as when a fish is left in a small volume of unchanged water), there is for a time increasing restlessness attended by a rising rate of respiration and greater frequency of spouting. In the cases closely followed, there were, early in the experiment, alternate periods of rest with slow respiration, and periods of activity with rapid respiration and frequent spouting. This behavior suggests that, as the fish rests normally for a time, it begins to suffer discomfort because of the deterioration of the water. There ensues, then, a brief period of moving about and rapid breathing and spouting. The momentary quickening of the respiration restores comfort and the fish sinks to rest again, soon to repeat the whole performance.

Later in the experiment the rate of respiration was continuously high, with frequent spouting.

At the near approach of asphyxia the rate of respiration gradually diminishes, but spouting continues to occur with greater frequency than under normal resting conditions.

In recovery from asphyxia respiration was at first weak and slow, but during the first few minutes of the period of recovery spouting occurred with very marked frequency,— up to five times in one minute. Within the first hour or two of the period of recovery the rate of respiration gradually rose and attained a maximum far above the normal rate in a resting skate, while the rate of spouting, after the first few minutes of excessive frequency, gradually fell, as the rate of respiration became higher. But so long as respiration continued at a high rate, spouting occurred with much greater frequency than under normal resting conditions.

Spouting Induced by Tactile Stimulation. Some chance observations led me to try the effect of tactile stimulation of the skin in the vicinity of the external spiracular aperture. When the margin of the spiracle was gently touched with the end of a glass rod or with a stiff bit of eel-grass there usually resulted immediately a spouting from both spiracles at once. But a sharper stimulation, or persistent annoyance of one spiracle, often resulted in a vigorous spouting from that spiracle only. When a spouting had once been provoked by tactile stimulation, the immediate repetition of the stimulation usually failed to produce a second spouting. But after an interval of several seconds had elapsed, renewed stimulation usually brought again the spouting response.

One skate was especially lively and responded to stimulation much more promptly and energetically than the others. This animal was experimented with for a brief time in a small tank containing so little water that the external aperture of the spiracle was submerged only about an inch. A fairly vigorous prodding of the skin at the margin of the spiracle by means of the sharp-pointed end of a bit of glass tubing resulted, in some twelve trials, in an extremely energetic spouting from the stimulated spiracle only. This one-sided spouting was provoked first from one spiracle and then from the other, in fairly rapid succession, by rather sharp stimulation of the spiracles alternately. The column of water

was squirted from the spiracle with such energy as to rise through an inch of water and some seven or eight inches vertically upward into the air. Frequently the stimulation was followed, not only by the spouting, but by a sudden dash to another part of the tank, as if to get away from the annoyance.

Tactile stimulation of the skin in the region of the eye also usually caused spouting. A gentle touch upon the outer corneal surface of the eyeball almost invariably provoked a particularly vigorous spouting from the corresponding spiracle. Indeed, stimulation of the cornea was found to be a more certain way of provoking spouting than stimulation of the spiracle itself. The response was always immediate and definite and in nearly every instance unilateral.

I tried also the introduction of solid materials of one sort and another into the gill chambers. I first tried sand, allowing a little to sift into the spiracle when it opened for an inspiration. Sometimes a spouting resulted, but equally often, even though a considerable quantity of sand was introduced, no response whatever followed.

Experimenting in a similar way with another fish, I found in the aquarium some shreds of filmy substance of doubtful nature. They appeared like bits of sloughed-off skin. It well exemplifies the impromptu character of all of these experiments that, making trial of whatever happened to be suggested by the materials at hand, I caused some of this doubtful filmy substance to be sucked into the spiracle at an inspiration. Invariably material of this sort was promptly expelled by spouting. Often one or two inspirations intervened between the one by which the foreign material was drawn in and the spouting by which it was expelled. Usually the spouting occurred from both spiracles at once,— rarely from only the one at which the foreign material was introduced. The material was always ejected by the same spiracle at which it entered.

In the one-sided spouting the action of the unstimulated spiracle appeared to be uninterrupted. The stimulated spiracle simply remained open during one closing of the other.

Summarizing the foregoing account, it appears that the spiracle of the common skate serves chiefly as an in-take for the respiratory

stream, but at somewhat regular intervals the stream is reversed and an expiration takes place via the spiracle, which thereby becomes a spout-hole. With quickened respiration due to exercise, the spouting occurs much more frequently than in the resting fish. Also, when a skate is confined in a small volume of water which is not changed, respiration is quickened and spouting occurs much oftener than under normal resting conditions. Whether in this case the higher rate of respiration is due directly to the condition of the water, or to the activity caused by the unfavorable quality of the water, I am unable to say. M'Kendrick ('79) states that, in the presence of an insufficient supply of oxygen the fish "breathes hurriedly." Finally, spouting occurs with excessive frequency in skates which are just beginning to recover from an advanced stage of asphyxiation. What, in view of these facts, is the probable rôle of the spouting, so far as it is a respiratory act? May it not be roughly analogous to "taking a deep breath"? An occasional reversal of the respiratory stream may serve to clear out the gill chambers, resulting in a more nearly complete change of water in them. The greater frequency of the spouting when respiration is quickened, by whatever cause, and its excessive frequency in recovery from asphyxia indicate, I think, that it has some importance in the way of increasing the efficiency of the respiratory process.

Spouting in response to tactile stimulation in the vicinity of the spiracle indicates that the fish may, under natural conditions, employ the spout-hole as a means of expelling foreign solid materials from the gill chambers, or of dislodging objects from the surface of the body in the region of the spiracles and eyes. The behavior in respect to sand puzzled me at first. Skates when resting on the sea-bottom have a habit of settling themselves into the sand and washing it over their backs in such a way that sand would, apparently, be very likely to sift into the spiracles, and one might suppose that sand would be particularly irritating. But in my experiments the skates were indifferent to the introduction of considerable quantities of sand, while soft filmy materials were promptly spouted out. On further consideration, it occurred to me that sand, being a finely divided substance, would easily wash out through the gill clefts, whereas, being heavy, it could not so

readily be forced up through the spiracles. But the larger fragments of soft material (such as bits of sea-weed) are likely to be caught on the gill-rakers, tending to clog the branchial passages, and could best be dislodged and expelled by a reversal of the currents.

The prompt, vigorous, and almost unfailing response to a touch upon the cornea suggests that the fish regularly employs spouting as a means of keeping the eyes unobstructed. The external opening of the spiracle is so near the eye that a stream spurted from the spiracle would readily wash away foreign objects which settle upon the eye.

Regarding the spiracle as one of a series of visceral clefts which were primitively similar in structural relations and in function, it is evident that, serving as it does such a diversity of uses, it has come to differ from the more posterior visceral clefts quite as markedly in its function as in its structural conditions.

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